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THE ANALYSIS OF NATURAL SELECTION¹

THE actual operation of natural selection is rarely investigated. The various methods that have been employed will be here considered seriatim, in order that their advantages and limitations may be noted.

1. The comparison of the mean magnitude of the characteristic in question in those individuals that died either with that of the survivors or with that of the whole number. This method is simple and where the difference is considerable does provide proof that secular² natural selection was operative. Its shortcomings are that it furnishes no analysis of the operation of selection and that periodic³ natural selection is not detected by it.

2. The index of correlation between the length of time of successful resistance to the adverse condition and the magnitude of the characteristic in question. This method has been used by Dr. F. E. Lutz on *Ampelophila*. In addition to demonstrating the action of natural selection, it may in some cases, as in *Ampelophila*, throw valuable light on the action of the cause of death. Its limitation is its failure both to discriminate between periodic and secular selection and to analyze the distribution of the incidence of natural selection.

3. In addition to comparing the means of the individuals that perished and survived, Bumpus, in his well-known sparrow observation, compared the extremes with the whole number, in this way being able to detect any periodic selection that may have taken place, as well as the secular selection. This method, too, falls short, because a still closer analysis is desirable, and because the result hinges on the particular choice of the percentage of the whole chosen to represent the extreme.

4. We have a further step in analysis in

Weldon's method of showing the results of his classic experiment in subjecting *Carcinus* to clay suspended in water. Here the polygon of the perished is superimposed upon the polygon of frequency for the whole number. The eye can then wander along the polygons and observe the relation of the two throughout their courses, which makes a fuller analysis possible. But in making the analysis the mind must compute the ratio for each class as best it can.

The method which I wish to propose determines these ratios precisely and plots them graphically. The survival rate is determined for each class, and plotted, preferably superimposed upon the polygon of frequency of the whole number, so that the numbers used are shown. Since the probable error of the survival rates increases towards the extremes where based upon fewer individuals, some method of combining classes is frequently desirable. Only such combining should be done as is considered absolutely necessary, because the analysis is less discriminative by just so much. The combining may be done by arbitrarily adding the classes in groups of 2, 3, 4, etc., or by combining the most extreme eighth in one direction, the next eighth, and so forth. This may be done absolutely, or in some cases, to the nearest class. The particular method depends largely upon the number employed. Rougher grouping and a larger number of classes are permissible where there are large numbers. In Fig. 1 I have applied the method to Weldon's experiment with crabs (male *Carcinus mœnas*) in muddy water. The survival rate is determined for each class and a survival curve thus established. It will be seen that, even with this large number of classes, the curve is clearly inclined. In Figs. 2 and 3 I have replotted the curve in four and eight classes, respectively, of about equal numbers to smooth out the irregularities arising from the small numbers in the extreme classes. With so active a natural selection, one can well believe that, in spite of the criticism of Cunningham, there actually took place in nature the evolution shown by the statistics gathered in the successive years of the crabs at Plymouth.

¹ This article was written while the author was on the staff of the Station for Experimental Evolution at Cold Spring Harbor, N. Y., of the Carnegie Institution of Washington.

² Pearson's term for the form of natural selection which favors one extreme over the other.

³ Pearson's term for the form of natural selection which favors the mode at the expense of the extremes.

The numbers are smaller in the widely quoted observations of H. C. Bumpus on the sparrows which survived in a lot that were picked up after a severe storm at Providence, R. I. By using only four classes, however, the survival curve is so inclined that we may safely draw conclusions. The conditions in

other measurements to percentage of length. The result shows a much greater influence of selection than that shown by the absolute measurements. The selection is also seen to be secular (Fig. 5) rather than periodic, as Bumpus concluded from the absolute measurements. The survival curves are shown for the

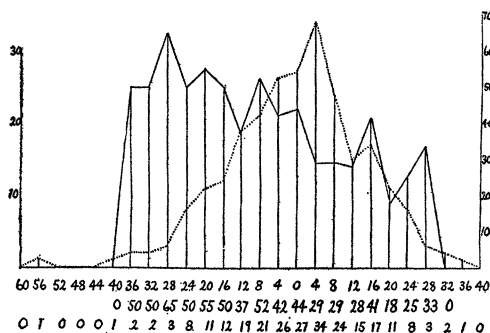


FIG. 1. The polygon of frequency of the frontal breadth (dotted line) of *Carcinus maenas* in Weldon's experiment, with the survival rate (solid line). First line of numbers, deviation; second line, survival rate; third line, numbers.

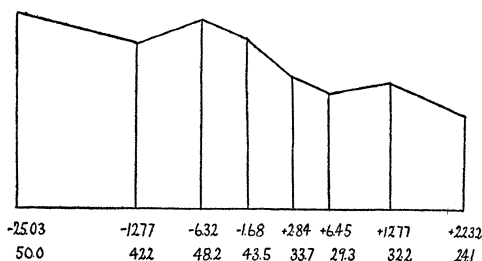


FIG. 2. The survival polygon in the Weldon crab experiment plotted in eight classes. First line of numbers, deviation; second line, survival rate.

this study probably do not show the full selective effect of the catastrophe, for we here contrast those which perished with the disabled which survived when protected. The sparrows which had succeeded in finding suitable shelter would probably have shown a still greater difference from those that died, could they have been obtained. Bumpus confined himself to a study of the absolute measurements, but since there was a selection as to the size of the birds (Fig. 4) I have reduced the

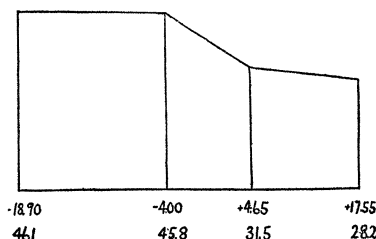


FIG. 3. The survival polygon in the Weldon crab experiment plotted in four classes. First line of numbers, deviation; second line, survival rate.

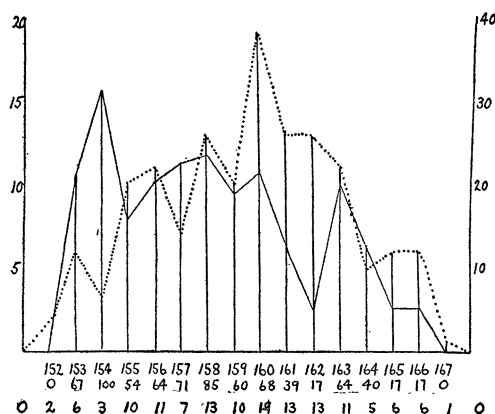


FIG. 4. The polygon of survival rate of the length in the Bumpus sparrow case. First line of numbers, length in millimeters; second line, survival rate; third line, number of individuals.

sake of direct comparison in one diagram, using as ordinates the average of the respective classes.

Curiously enough, while the males show a well-marked secular selection in the same direction in each measurement, the females are either only slightly secular or indifferent. In some cases, like the measurements of the femur and humerus of the males, the differences are very great, all of the longest fourth

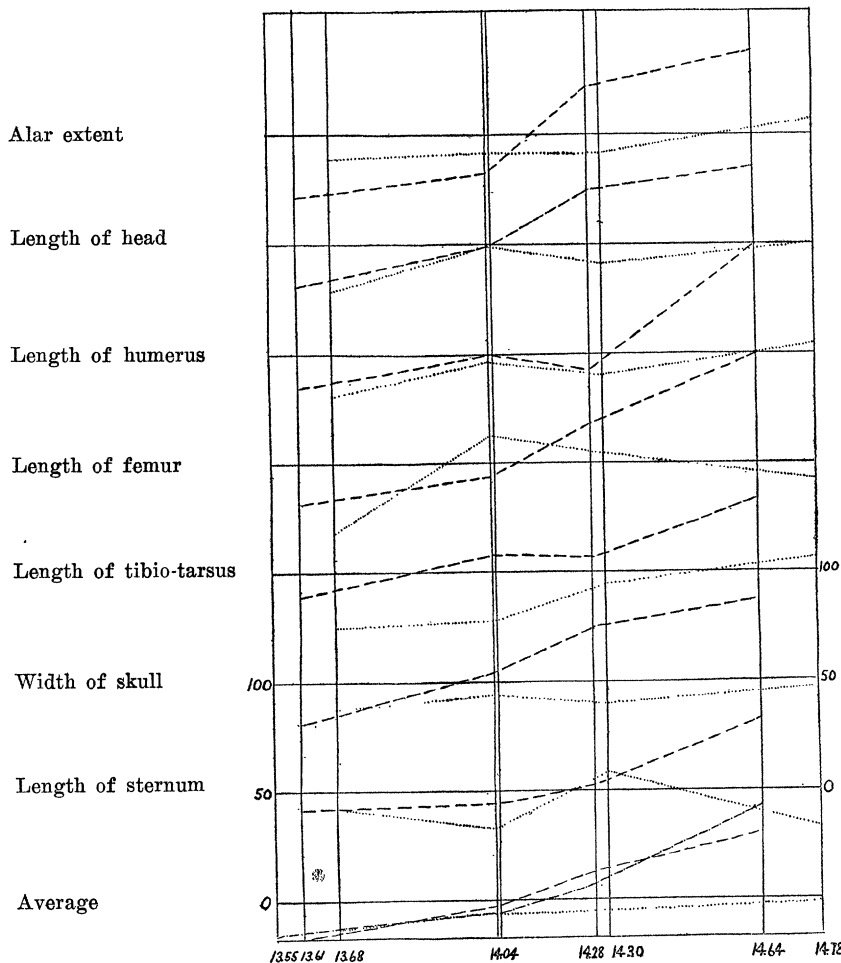


FIG. 5. The survival polygons of the measurements expressed in percentage of length in the Bumpus sparrow case. Dash line, all males; dotted line, females; dot and dash line, young males. The horizontal line opposite the name of each dimension represents 50 per cent. survival, the next horizontal line below 0 and the next above 100. Numbers at bottom are the average dimensions of the four classes.

(divided to the nearest class) surviving. Bumpus had based his conclusions on the very few extreme individuals, instead of the two extreme fourths. I believe this is dangerous, on account of the small numbers, but for comparison, I have also plotted the extreme classes. To avoid the danger of small numbers, I have combined the extremes in all six characteristics, since the survival curves have a common inclination. Here also the result (Fig. 6) shows secular and not periodic selection.

Bumpus was led to his conclusion from the fact that in length there is some degree of periodic selection as well as secular selection shown (Fig. 5). Even in length the small numbers involved in the end classes cast some doubt as to their significance. Taken as a whole, therefore, I believe this sparrow catastrophe reveals very much more secular than periodic selection, if there be any of the latter, although very naturally the experiment has been quoted to show periodic selection in the

literature of evolution, where it has figured so largely.

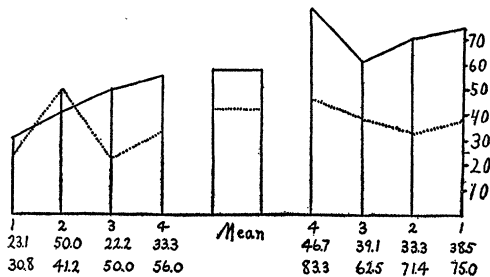


FIG. 6. The survival rate in the extreme cases in the Bumpus sparrow case to test periodic selection. The rates plotted are the rates made up by averaging those for the corresponding extreme classes of all the dimensions, each expressed in percentages of length. First line of numbers, the extreme classes; second line, survival of females; third line, survival of males.

The weight of the sparrows shows a secular selection in a negative direction, but in percentage of length, the selection seems indiffer-

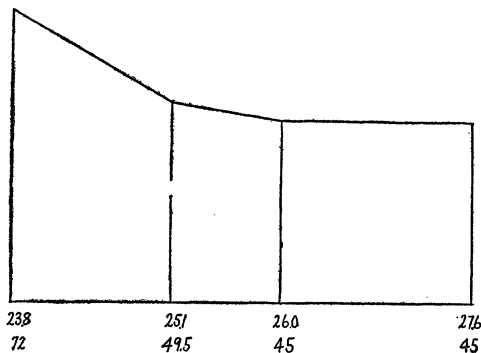


FIG. 7. Survival polygon for weight in the Bumpus sparrow case plotted in four classes. First line of numbers, weight in grams; second line, survival rates.

ent. The selection in absolute weight, therefore, is due to the correlation with length which is selected. For this reason and because it is not a dimension, I have not plotted it with the other characteristics (Figs. 7 and 8).

The application of this method to Cramp-

ton's observations on the length of antennæ in female pupæ of the moth *Philosamia cyn-*
thia, is shown in Figs. 9 and 10. This shows clearly the amount of selection and brings out the fact, which is otherwise overlooked, that

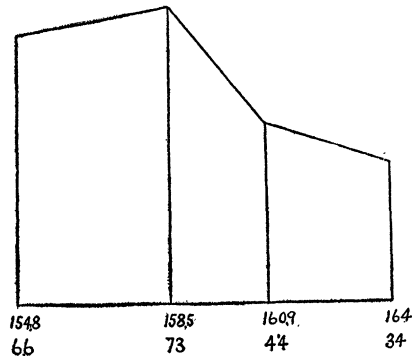


FIG. 8. Survival polygon for length in the Bumpus sparrow case plotted in four classes. First line of numbers, length; second line, survival rate.

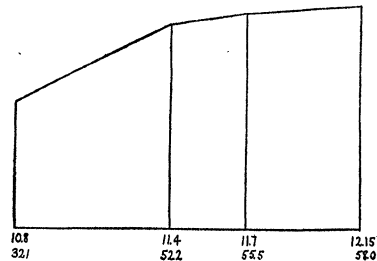


FIG. 9. The survival polygon of the length of left antennæ in female pupæ in Crampton's experiment plotted in four classes. First line of numbers, length of antenna in millimeters; second line, survival rate.

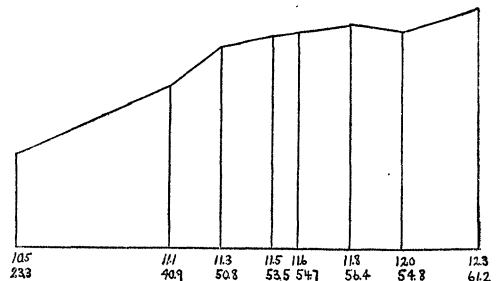


FIG. 10. The survival polygon of the length of left antennæ in female pupæ in Crampton's experiment plotted in eight classes. First line of numbers, length of antenna in millimeters; second line, survival rate.

the rate of survival changes most rapidly with the shorter antennæ.

Dr. Robert W. Hall and I have submitted *Palæmonetes vulgaris* to changed salinity. Figs. 11 and 12 show that where the marine

some of these brackish water shrimp were subjected to brine the survival curve was higher for the larger number of spines; that is, higher

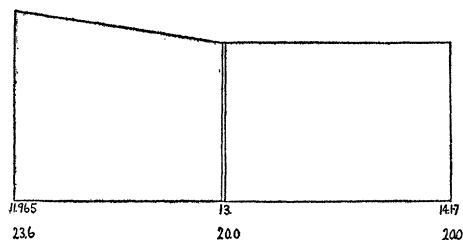


FIG. 11. Survival rate in Johnson and Hall experiment in exposing shrimp from marine salinity to fresh water. First line of numbers, number of rostral spines; second line, survival rate.

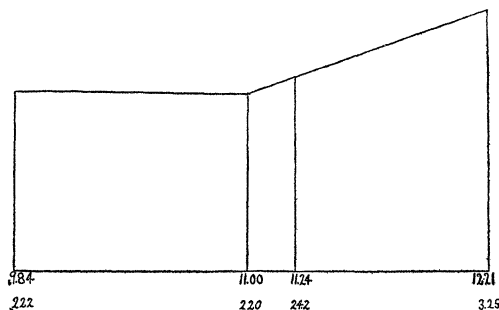


FIG. 12. Survival rate in Johnson and Hall experiment in exposing shrimp from brackish water to brine. First line of numbers, number of rostral spines; second line, survival rate.

shrimps were placed in fresh water, the survival curve is higher for those of few rostral

for the marine conditions. The difference in the former case not being well marked, the ex-

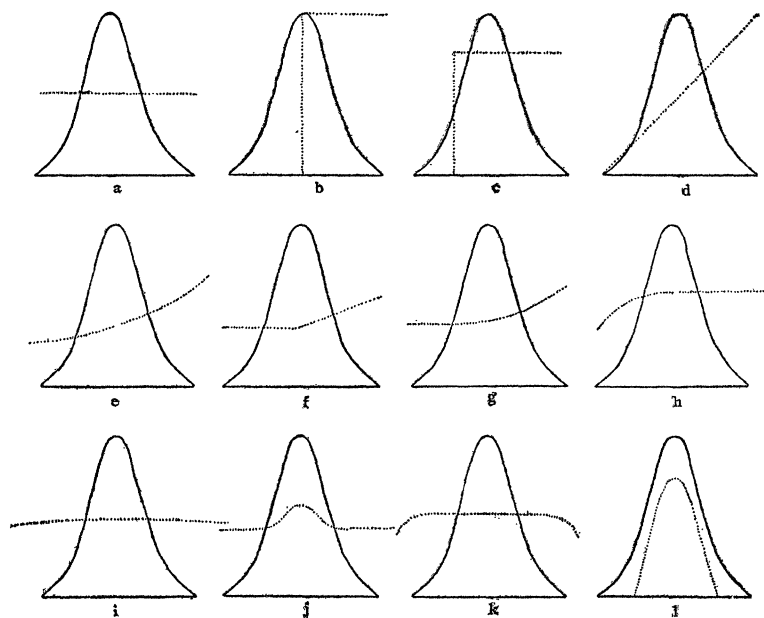


FIG. 13. Various theoretical survival curves (dotted) plotted upon a theoretical polygon of frequency.

spines. Few spines is the normal condition in the fresh water species. The brackish-water strain of the marine species has also fewer spines than the typical marine species. When

periments should be repeated on a larger scale and with greater refinements, before drawing definite conclusions. In the latter case, however, the result clearly shows selection.

In the use of the method in actual cases, the scale is of definite quantities. For theoretical purposes, we may plot survival on a vertical scale from 0 to 2. In this case 0 means no survival, *i. e.*, all individuals in the specified class died prematurely. At 1, we have one individual attaining the age of reproduction for each corresponding parent. At 2 we have two progeny attaining maturity for each corresponding parent. Now if the survival line is level (Fig. 13*a*) natural selection is not active;

some low value in the other direction, and at some point between rise to a point or become level as in Figs. 14*b* and 14*c*. In the case of Fig. 14*c*, the species will evolve until selection becomes periodic, but in Fig. 13*b* we have a different condition. Here it is carried to a point where natural selection becomes impotent. It is in such a case that determinate evolution has free play and may, in some cases, carry the species further. In still other cases there is an absolute limit of variation in the

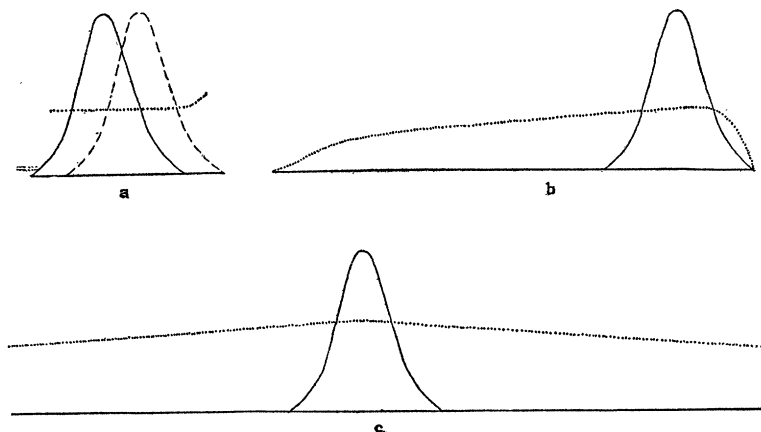


FIG. 14. Theoretical survival curves. Dotted line, survival rate; solid line, theoretical polygon; dash line, polygon of frequency of young individuals.

but if it be in any degree inclined (Fig. 13*d*) natural selection is in operation. Figs. 13*b*, 13*c* and 13*f*, I have drawn the survival curve as one would expect it from some descriptions of the action of natural selection, but such abrupt changes in the survival rate must be decidedly exceptional. The actual line is ordinarily a gentle curve, the survival rate always being low and gradually becoming lower or higher from class to class, as in Figs. 13*d*, *e* and *g-l*. The periodic selection where the species is kept stationary is illustrated in Figs. 13*i* to 13*l*. There is every gradation of course between this and secular selection. The point to which selection would carry the species might be close to the present mode.

The survival curve, if we had the data to construct it for a sufficient length, would probably, in many cases, especially those involving measurements, touch 0 in one direction and

characteristic; for instance, blackish color would have a limit at absolute black (Fig. 15*b*). In such a case the survival curve would come to a sudden stop on the particular rate for that point. If the inclination is upward

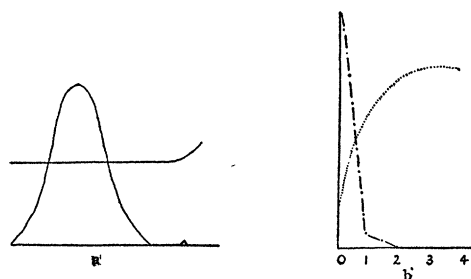


FIG. 15. (a) Theoretical survival curves with the mutation alone affected by a differential survival rate. (b) The polygon of frequency and of survival rate are limited in one direction.

toward the limit, the species must remain at the limit.

The process of natural selection must be further analyzed because of the heterogeneity of the species. A species is made up not only of individuals of two sexes in most cases, but also of individuals of various ages. This difference may affect the survival results in two different ways. The individuals of one sex may differ quantitatively so that they will be affected by differing survival rates when survival is discriminative. Because of the sexual difference, Weldon in his *Carcinus* experiment used males only, in order that it might not be necessary to increase the number to be measured.

At different ages, natural selection must often operate differently, for the characteristic changes quantitatively, and sometimes qualitatively, with age. Where the change is quantitative, the individual will change in its survival chance, where survival is discriminative. Where the change is qualitative the characteristic in question may only be in evidence during part of the lifetime. In addition to this, the survival chance may change with age, regardless of the magnitude, because of the general inefficiency of the immature. In many species, the rigor of natural selection is doubtless concentrated on the younger stages, with much decreased action later. Specific instances we have in the vital statistics of man, and in the large birds of prey, where they are not molested by man.

In experimental work, economy of effort demands concentrated attention upon adults only or upon the young of some restricted age group. Nevertheless, such a study has a serious limitation, for the whole influence of natural selection upon a species can not be known until we have an analysis of its action for every age group in the species. While the number of young individuals in the sparrow experiment of Bumpus was too small to permit an analysis along age lines, yet inspection shows that the selection was affected by age. It is quite probable that where natural selection is inoperative upon adults, it may be very efficient in some younger stages. In Fig.

14a I have illustrated the escape from the incidence of natural selection by age. Crampton's results with the antenna lengths of *Philosamia pupæ* might not be found to apply in imaginal life. In fact, we have the possibility that natural selection might be nullified by a reversal of action in the adult from its action at some younger stage. Thus an extra abdominal segment might be favored in the caterpillar, but penalized in the moth. Such a disparity has the effect of making the young different from the adult, ending in some cases in an elaborate metamorphosis.

It would seem that a polygon of frequency would move along a survival curve based upon the measurement of some one character until it reaches its summit, when it would remain stationary. Periodic selection would then ensue. This maintains the species at a fixed point and decreases variation. One might at first suppose that when a new structure begins, the survival curve would start at 0 and move along with the increase of the structure to a maximum. But it must be remembered that this is impossible, for the height of the theoretical curve must always have an average height of at least one, no matter what the characteristic used in the construction of the curve may be, unless the species is decreasing in abundance. Furthermore, it can get no higher than one unless the population is increasing in numbers. What we really have, therefore, when there is no change in abundance, is a compensatory depression of the whole survival curve, as the frequency polygon moves up its slope. It may be likened to a man climbing a step ladder in a descending elevator. His rate of speed might be such that his elevation would not change, but he would have horizontal motion. In this case, there would be a general depression of the survival curve to compensate for the increased survival from the increase of the characteristic in question. Elimination would necessarily become sharper at some other point, the weakest point, or at several weak points. But the elimination, discriminative with respect to this second weak characteristic, would with the first characteristic be generally distributed,

and so cause the general depression of its survival curve. For instance, let length of feather have a differential survival value, when a species of sparrow encounters colder winters. Evolution in the direction of increased feather length would cause an increased abundance of the species, unless there was a counter-influence. Such a counter-influence might be a greater mortality from shrikes, as more sparrows would thus come under their observation and engage a larger share of their attention.

The graphic method here proposed is also applicable to mutation (in the De Vriesian sense) though of less value in that connection. In such cases the mutation is plotted on the base line at the appropriate distance from the polygon of frequency and the curve of survival is extended past this point. The curve of survival may be level in the region of the polygon, but inclined outside of it, so as to affect the mutation either favorably or unfavorably (Fig. 15*a*). Or the survival curve may be inclined throughout its course, in which case the mutation does not have an exclusive advantage or disadvantage. Many of the complications referred to before are also applicable here, but further mention will only be made of the case where the survival curve is strongly inclined at the magnitude of the mutation and it is therefore strongly subjected to natural selection within its own unit in addition to its competition with the old species.

Coincident selection, which many zoologists have apparently had difficulty in understanding, is, I believe, made quite clear by the use of this method. I follow Gulick in considering Lloyd Morgan's term of coincident much preferable to Baldwin's meaningless phrase of "organic selection." In expressing coincident selection, it is only necessary to construct with the survival curve two polygons of frequency, one for the innate variation, and the other for the resultant variation after the modification by the environment.

The action of coincident selection will differ in degree according to the type of correlation of the modification with the innate

variations. There may be three cases. In the first, the modification is always the same in amount, regardless of the degree of development of the innate character. This results in the transfer of the original polygon of frequency to one side or the other. Since, however, the modification would of course be some-

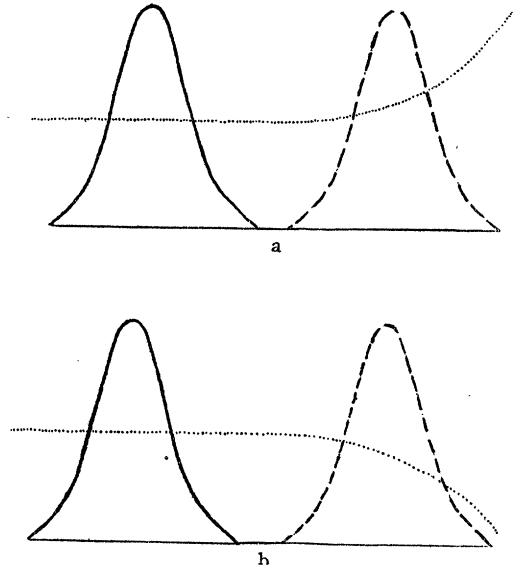


FIG. 16. The dash line polygon represents the individuals in a case of extreme coincident selection after modification. The solid line polygon represents the individuals as they would have been if not modified. Dotted lines are theoretical survival curves.

what variable, there would be some readjustment of distribution, and a corresponding increase of the variability (Fig. 16*a*). This is the case usually assumed in the consideration of coincident selection and its consequences are well known. In Fig. 16*b*, where the modification is opposed by natural selection, it may be expected to decrease in amount. In the second case, the modification is greater in those individuals which have the innate characteristic in a less degree than in those in which it was larger. Thus, elephants with an innately shorter trunk might have greater modification than others because of greater strains involved in its use. The final result in this case, then, would be the shifting of the

left end of the polygon of frequency further to the right than the right end would be shifted. This produces a narrowing of the range and decrease of variability (Fig. 17*a*). The result is a decrease of natural selection, unless the survival curve is more inclined at the new position (Fig. 16*b*). In the third case, those with the characteristic in question innately larger sustain the greatest modification. This might be illustrated in the case where only some moths which could reach the nectar of a particular flower would make con-

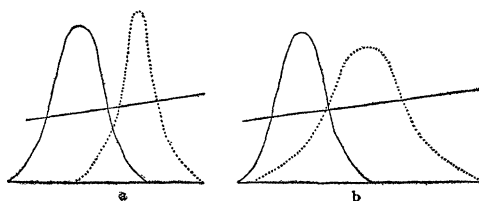


FIG. 17. The straight solid line is the survival rate; the dotted line, the polygon of the individuals as modified. To illustrate action of coincident selection in decreasing and increasing variation.

tinued effort to do so. By increasing the range (Fig. 17*b*) an increased efficiency of natural selection is produced, even though the polygon is not transferred to an increased inclination of the survival curve. It is probable that the greatest importance of coincident selection lies in its efficiency to promote incipient organs in this way, for it is easy to see how important it would be in such a case as the transformation of a somewhat prehensile snout to the elephant's trunk. On the other hand, it must, in many cases, slow up the efficiency of natural selection, when an organ has passed the "infant industry" condition, and thereby enters the second category referred to.

The study of the analyses which have been presented brings out some facts as to correlation of characters which should be mentioned here. It is often assumed that every character that is selected has a direct survival value. Some authors have recognized that a characteristic may be carried along by correlation with some related characteristic which has survival value. In these cases, the correlated

characteristics are generally thought to be two distinct structures, for the correlation of which a reason is evident. It will be noticed, however, that in the case of the sparrow catastrophe, the several dimensions, aside from the length, are all selected in the positive direction and that they are all dimensions of head or limbs except the length and one body measurement, which is taken in the cephalo-caudal direction. The one characteristic not of this sort, weight, had an indifferent survival value. If we try to reason out particular advantages in each of these character changes, we are hard pressed.

Is it not probable that they are all correlated with a physiological characteristic or two, which has its external manifestation in a general increase of peripheral parts and slenderness? This is not fantastic, for we have something analogous in human pathology. The disease of acromegaly, caused by some condition of the pituitary body, produces a great increase in height and in the size of the hands and the feet. The survival value of length of antennæ in moth pupæ, the number of rostral spines of a shrimp, affected by changed salinity, are inexplicable on the basis of direct adaptation. We are driven to resort to correlation with internal features. But the frequency with which this resort to correlation is necessary in the discussion of the experiments on survival values seems significant. Even in case of the frontal breadth of the crab, where a definite value has been postulated, namely, that the narrowness of slit which permits water to reach the gills may be of importance in excluding mud, we are still dealing with a correlated character.

The multiplicity of structure that we find in animals, particularly in sculpture and markings, is simply bewildering, if we consider them all as adaptations. But with an appreciation of the great rôle played by correlation in natural selection, we should expect just such a wonderful maze of characteristics. Just as our modern insistence on the importance of the variations that offer themselves reduces the creative rôle of natural selection,

so does it become further reduced by emphasis on the importance of correlation, rather than the direct usefulness of the characteristic in question.

Of course, it is unfortunate to be obliged to find that so much of importance in evolution is not to be found in the more easily understood and investigated work of direct selection. It seems like a step backward, to be obliged to conclude that not only do we know less than we thought we did, but to also have important avenues of investigation either closed or made very difficult. It bewilders us to realize that the most fundamental factors of evolution lie in the abstruse, deep-lying problems of the origin of variations and their correlations. A gleam of promise lies in the recent induction of variations by Tower and MacDougal. Epochal as these results are, they may be said to be more the evoking of variations than the making of them. The greatest promise for light on the origin of correlation probably lies in the study of internal secretions and in the transplantation of tissues and organs.

This position in reference to correlation has its significance for the guidance of further experiments on survival values. I do not believe it is necessary to pick out obviously adapted characters for selection experiments. In proper analysis with large numbers, most causes of death will probably show discrimination with most characteristics. We may, therefore, expect to get appreciable results in aquatic animals by altering salinity or carbonic dioxide content or muddiness, and in terrestrial animals, by altering temperature, humidity, etc. On the other hand, there should be care in selecting the species with reference to the following conditions:

1. The animal should be readily obtainable in great numbers.
2. The sexes should be readily distinguishable.
3. The adverse condition should be capable of being applied evenly to any desired degree with the least possible alteration of other conditions.

4. The species should have an allied variety or species living in the new environment, which differs from it in the characteristic chosen.

5. The characteristic should be one easily measured or counted and show a good range of variation. Measurements should be ordinarily expressed in percentage of length.

6. The characteristic should not change with age, or at least not within some adult size unit to be used.

7. A further advantage lies with a species capable of being successfully bred. It may become desirable to get light upon some point by this method.

Of course natural selection is determined not by the death rate at any one catastrophe, but by the end result of the various vicissitudes that all the individuals of a species pass through from the laying of the egg to the completion of reproduction. It is therefore dangerous to conclude that the natural selection seen in any of these experiments, which all express the result of a part only of the life of the individuals, was actually producing evolution in these species. Of course, diagrams such as these must not be expected to give the entire evolutionary status of a group of individuals. We may have such a condition as shown in Fig. 17 and still have the species stationary, for the advantage in one direction may be much reduced or wholly lost by selection in the opposite direction in some other catastrophe or critical period of life. Thus, long antennæ were favored in the pupæ of *Philosamia cynthia*. It is quite possible that short antennæ might be favored in the imago, for conditions are so dissimilar. Slenderness was an advantage to sparrows in a blizzard, but compactness might be in dodging hawks. The lethal selection may also be counteracted by sexual or fecundal selection, modification of the germ plasm, or orthogenesis. For a time any one of these influences may even force the species in the opposite direction to that in which lethal selection is impelling it.

The relation to orthogenesis is especially

interesting. Orthogenesis is a progressive variation or biased heredity in a given direction in successive generations. It is not a constant process, but one which is active in a certain characteristic in a particular species for a limited time, while most other characteristics are untouched by it. Let us call one of these lines of orthogenetic activity an "orthogenetic run" after the analogy of the "run" on a special line of merchandise which merchants occasionally experience. In such an orthogenetic run the individual steps are often not affected by selection up to a certain point, or only to so slight a degree as to be relatively negligible. But a "run" may eventually reach the threshold of a decisive selective value. Natural selection will then stop the course of the run. The "run" may be eradicated from the species, or when it is too persistent to be eradicated, then the species will be exterminated, as I imagine has taken place in the Irish elk and in the excessively spiny species with which many extinct mollusc genera have culminated.

But the result of such continued checking of inimical runs and the tolerance of other neutral or beneficial runs is to determine to some degree the kinds of "runs" that will arise in the future. Thus "runs" dealing with distribution of hair and hair modifications in great variety have been tolerated or encouraged, so that runs of this kind became commoner. On the other hand, runs affecting the chemical constitution of the red blood corpuscle once it had reached the vertebrate standard have been so promptly checked that variation in this characteristic has been checked and a high degree of conservatism resulted.

The analysis of the experiments given has a further value in its bearing on the question of the possible selective value of minute variations. Indisputably there has been too general a faith in widespread selective values in the past. At present, however, we can see evidences of an unjustifiably extreme reaction. In the consideration of selective values, critics have been wont to compare two adja-

cent classes of the frequency polygon and to descant on the improbability of a selective value. A safer viewpoint is to consider the chances of two classes not immediately adjacent. If a selective value is found between some two classes, we may be fairly sure that the selective value will not end abruptly, but become less step by step in passing from one class to the other. It is absurd to expect a high survival rate in one class and a low one in the next. In almost all cases we must expect the survival rate to gradually increase or diminish from class to class. This is the verdict of the experiments. It is idle to talk about the impossibility of selective value of minute differences, when it is possible to measure and analyze them.

The object of this paper has been to develop the method of analysis of natural selection by the construction of survival curves, in order, first, to extract more meaning from the experiments already performed, but second, and especially to encourage further selection experiments by making it possible to obtain more significance from them. Its publication has been delayed four years that the author might add some applications of the method. Occupation upon another line of research makes its publication necessary now without such results in the hope that they will be supplied by others.

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SPECIAL ARTICLES

BOTANICAL EVIDENCE OF THE AGE OF CERTAIN OX-BOW LAKES

In the southeasternmost county of Arkansas, near the Mississippi River, there is a crescent-shaped ox-bow lake about 15 miles long, of a type frequent in the flood-plains of large sluggish rivers, known as Lake Chicot. Lake Village, the county-seat of Chicot County, is located on the side farthest from the river, and the railroad from that point to Luna Landing on the Mississippi skirts its northern bank for a few miles. At present the shores of this lake are mostly pastured, but at